

DIVERGENT TRANSFORMATION OF CHELICERAE AND ORIGINAL ARRANGEMENT OF EYES IN SPIDERS (ARACHNIDA, ARANEAE)

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In various higher taxa of the Araneae (e.g., Mesothelae, Migidae, Hypochilidae), the chelicerae and their fangs show an intermediate position between those commonly called orthognathy and labidognathy. This stage is considered to form part of the ground pattern of spiders; accordingly, it is called plagiognathy (new term). It is concluded that plagiognathy gave rise to orthognathy and labidognathy as divergent adaptational developments. In most instances, plagiognathy is correlated with the maintenance of the original (plesiomorphous) arrangement of the lateral eyes (= ALE + PLE + PME) in triads or semi-triads. The previous assumption that orthognathy and the arrangement of eight eyes in two subparallel rows are characters that were already present in ancestral spiders is refuted.

Bei verschiedenen höheren Taxa der Araneae (z.B. Mesothelae, Migidae, Hypochilidae) weisen die Cheliceren sowie deren Klauen eine intermediäre Position zwischen Orthognathie und Labidognathie im üblichen Sinne auf. Diese Anordnung wird als Teil des Grundmusters der Echten Spinnen angesehen und hierfür die neue Bezeichnung Plagiognathie eingeführt. Von diesem primären plagiognathen Zustand werden sowohl die Orthognathie als auch die Labidognathie als divergente Entwicklungen mit unterschiedlichem Anpassungswert abgeleitet. In den meisten Fällen ist Plagiognathie korreliert mit dem Erhalt der ursprünglichen (plesiomorphen) Anordnung der Seitenaugen (VSA + HSA + HMA) in Form von Triaden oder Semi-Triaden. Die bisherige Annahme ist nicht länger aufrecht zu erhalten, wonach Orthognathie und die Anordnung von 8 Augen in zwei Querreihen als Komponenten des Grundmusters der Spinnen angesehen worden waren. □ *Araneae, plagiognathy, orthognathy, labidognathy, lateral eyes, triads.*

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It is generally believed that the chelicerae in spiders can be arranged in either of two different ways, described by the terms orthognathy and labidognathy. Orthognathy is commonly thought to represent the primitive (plesiomorphic) character stage (Foelix, 1982: 3; Platnick and Gertsch, 1976: 13). At first glance, this view seems to be supported by the fact that a strictly orthognathous arrangement of these mouthparts is also present in the outgroup of the Araneae, i.e., in the Amblypygi. Hence, the idea that orthognathy is a plesiomorphic feature seems to be the most parsimonious explanation. Accordingly, labidognathy is regarded as a derived (apomorphic) feature. Kaestner (e.g., 1952, 1953a, b) presented arguments supporting the assumption that labidognathous, i.e., cooperating chelicerae had various functional advantages. He produced a model (Fig. 1) illustrating the transformation of a 'primitive' orthognathous arrangement into the labidognathous position. However, it is difficult to imagine how this could have happened gradually, and Kaestner did not explain why or-

thognathy had been maintained in a considerable number of higher taxa.

Simon (1892: 64, 82) pointed out that the Liphistiidae and Migidae had arrangements of the chelicerae that did not fit very well into the generally accepted orthognathy/labidognathy scheme. Later authors ignored such 'deviations', however, and continued to base the distinction of two major subtaxa of spiders—Mygalomorphae (=Orthognatha) and Araneomorphae (=Labidognatha) on different positions of the chelicerae. Kaestner alone remarked on the intermediate arrangement of these mouthparts in Actinopodidae and in *Hypochilus*, but apparently he too continued to adhere to the typological orthognathy/labidognathy concept. One main aspect of his study was therefore to classify the chelicerae in *Hypochilus* as orthognathous or labidognathous.

In this paper, we will present relevant facts, most of them already known for decades, and discuss conclusions allowed by alternative concepts.

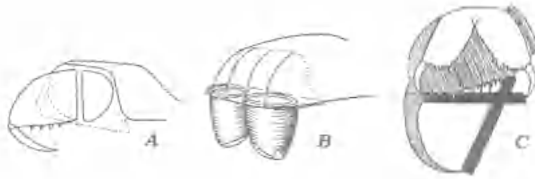


FIG. 1. Transformation of chelicerae as supposed by Kaestner. A, orthognathy, left chelicera omitted, front of prosoma nearly vertical. B, labidognathy, dotted lines and arrows indicate how front of prosoma (with chelicerae) shifted from original vertical to a horizontal position (rotation of basal segments of chelicerae not indicated). C, suggested economy of relatively small cooperating labidognathous chelicerae compared with a single orthognathous chelicera (hatched); both seize objects of same size.—(From Kaestner, 1953b).

This approach leads directly into a critical discussion of another generally accepted dogma in arachnology—that the eight eyes present in the ground pattern in spiders were originally arranged in two more or less parallel rows. In the nearest outgroups (Amblypygi, Uropygi), however, the arrangement of these eight eyes is quite different: the lateral eyes form triads on both sides of the prosoma. Such triads also occur in certain spiders. We therefore also plan to adopt a somewhat unconventional approach, discussing the question as to whether the presence of such triads in various subtaxa of the Araneae could be a persisting plesiomorphic character expression.

RESULTS AND INTERPRETATIONS

CHELICERAE

FACTS.

Orthognathy is commonly regarded as plesiomorphic. However, precisely those spiders that have the greatest number of plesiomorphies in common (Platnick and Gertsch, 1976) do not show an orthognathous position of their chelicerae: in the Liphistiidae (Figs 2a-b) the basal segment (paturon) of these mouthparts is relatively short, inflated and obliquely positioned. Further, the longer axis of this basal segment is orientated obliquely downwards, and not horizontally and paraxially as in 'true' Orthognatha (Figs 2c-d). The corresponding position of the fangs is also oblique, and anything but paraxial, in contrast to the position of the fangs in *Atypus*, for example (see Simon, 1892: 64).

The same situation as in *Liphistius* is also found in various subtaxa of the Mygalomorphae. In 1892, Simon (: 82) described similar arrange-

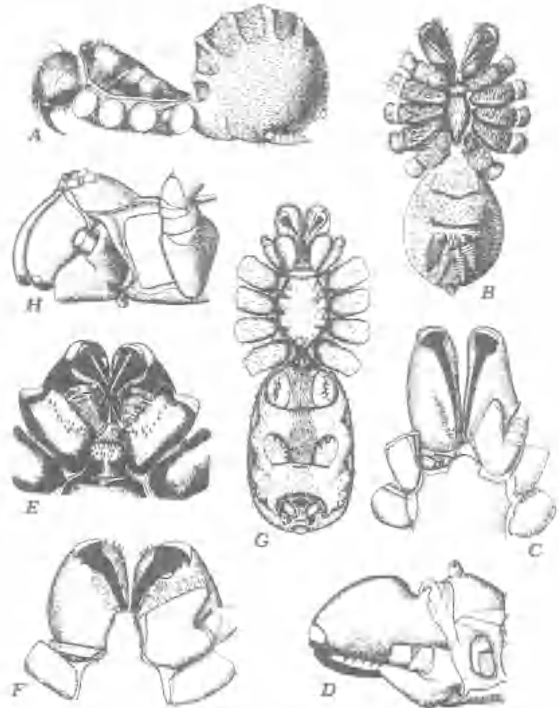


FIG. 2. Position of chelicerae and fangs, lateral and ventral views. A-B, Mesothelae: *Liphistius* sp. C-D, Atypidae: *Atypus affinis*. E, Migidae: *Migas quintus*. F, Actinopodidae: *Missulena occatoria*. G, Hypochilidae: *Hypochilus gertschi*. H, *H. thorelli*.—(A-B from Millot, 1949; C-D, F, H from Kaestner, 1952; E from Wilton, 1968).

ments in the Migidae, referring to 'chelicères très courtes, convexes à la base, mais ensuite brusquement inclinées, presque verticalement ...' (see Fig. 2e). Kaestner (1952: 118) studied *Sason robustum* (O. P.-Cambridge, 1883) as a representative of the Barychelidae and characterized the chelicerae as short and subvertically inclined. In the same paper, Kaestner demonstrated that obliquely arranged chelicerae were also present in the Actinopodidae (Fig. 2f); he described the situation in *Missulena occatoria* (Walckenaer, 1805) and concluded: 'I cannot see any biological reason for such conditions. But as torsions of this kind play an important role in the origin of labidognathy, it is interesting to see that they [the torsions] may also occur in the Orthognatha' (transl. from German).

It is worth mentioning that the chelicerae even of the oldest known spider, *Atterocopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (Middle Devonian), had short basal segments and also fangs (Selden *et al.*, 1991, e.g., plate 1, figs 6-8).

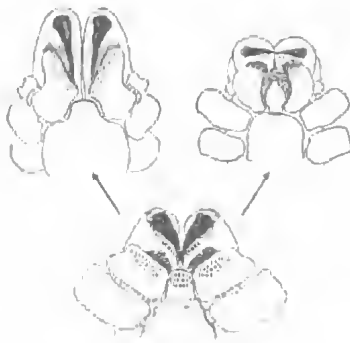


FIG. 3. Orthognathy (left) and labidognathy (right) as apomorphic character states derived from plagiognathy (bottom).

Unfortunately, their original position is unknown.

Chelicerae with an oblique position are also found in a taxon that unquestionably belongs to the Araneomorphae (= Labidognatha *auct.*): the Hypochilidae (Figs 2g-h). Again, it was Kaestner (1952: 132) who studied details. He concluded that the mouthparts in *Hypochilus* were of the orthognathous type in construction and expressed the view (Kaestner, 1952: 114) that 'the majority of important characters present in *Hypochilus* is in accordance with the Orthognatha, whereas the number of features present in Labidognatha only is very low. For this reason, I must remove the genus from the suborder Labidognatha and either place it in the Orthognatha or set it up in a suborder of its own' (transl. from German).

INTERPRETATION

Kaestner maintained that labidognathy was an advanced character state, which had developed from an orthognathous ground pattern by gradual transformation (Kaestner, 1953a: 60; Fig. 1). He felt that *Hypochilus* (and the Hypochilidae) should be regarded as transitory stages and explained the oblique position also present in the Barychelidae and Actinopodidae as a parallel development. Furthermore, he regarded the 'semi-orthognathous' chelicerae in *Dysdera* (Dysderidae) as intermediate. Kaestner thought, then, that various transitory stages still existed, forming a 'phylogenetic link' between the two extreme character states.

We reject this judgement based on typology, and postulate that an oblique position of the chelicerae, including the fangs, really represents the plesiomorphic situation (Fig. 3). As a new term is needed, we would like to suggest 'plagiognathy' to designate this original position

of the chelicerae. Accordingly, the plagiognathous position present in the ground pattern of the Araneae has been secondarily transformed in two different directions, both apomorphic character states: orthognathy and labidognathy (Fig. 3). We see various arguments in support of this hypothesis:

a) It explains why orthognathy is not encountered in the Mesothelae (*Liphistius*, *Hep-tathela*).

b) The absence of orthognathy in representatives of several mygalomorph families is explained.

c) The fact that the Hypochilidae are not labidognathous is explained by the simple assumption that the original plagiognathy has been maintained in this group of the Araneomorphae. Nonetheless, in all other Araneomorphae (this means in the Neocribellatae, the sister taxon to the Hypochilidae) labidognathy has been achieved and is regarded as an apomorphy of this taxon. This conclusion is not invalidated by the fact that superficially orthognathous arrangements originated secondarily in a few sexually dimorphic araneomorph taxa (e.g., in males of the salticid genus *Myrmarachne*).

d) Kaestner's typological and entirely theoretical model suggesting how a supposed transition from orthognathy to labidognathy could come about (Fig. 1) is replaced by a new concept (Fig. 3). This postulates divergent and gradual evolutionary change of the ground pattern, that is to say, of plagiognathy.

e) Kaestner's complicated assumption that obliquely arranged chelicerae originated in parallel both in the Mygalomorphae and the Araneomorphae is replaced by a simple, comprehensive hypothesis.

The only remaining conflict seems to be that reflected in the strictly orthognathous position of the chelicerae in the most closely related out-groups of the Araneae (Amblypygi, Uropygi). If our 'plagiognathy hypothesis' is correct, it must be assumed that orthognathy in the Araneae is a different and thus independent secondary development within the mygalomorph spiders. There is no question but that this contradiction needs some further examination.

Preliminary investigations have already suggested that orthognathy in Amblypygi may be different from orthognathy in spiders: the basal segment in amblypygid chelicerae has a long, stout apodeme at its proximal dorsolateral border, which reaches deeply into the broad, flat prosoma. This peculiarity is lacking in plagiog-

gnathous and also in orthognathous chelicerae of spiders. We expect that more detailed studies on the functional morphology, including the musculature, will demonstrate that orthognathy in uropygids and amblypygids differs from orthognathy in spiders. This would support our view and could perhaps constitute point f) in the list of positive arguments above.

EYES

Surprisingly, plagiognathous spiders (for example Mesothelae, Migidae, Hypochilidae) share a special arrangement of the eyes (Figs 4g, e, c): anterior lateral, posterior lateral and posterior median eyes are grouped closely together. This prompts the following remarks on the question as to how the eyes were grouped in the ground pattern of the Araneae.

As designations widely used in taxonomic descriptions (AME, ALE, PME, PLE) disregard the origin of these 'ocelli', some notes on the homology of the eyes of spiders may be appropriate to ensure that we understand each other. The anterior median eyes (AME) will be called 'median eyes' by us, as they are homologous with the median eyes of other arthropods (for example those in Xiphosura, 'ocelli' in insects, and the three components of crustacean nauplius eyes). All other eyes, three on each side, will be called 'lateral eyes' (ALE + PLE + PME), as they are homologous with the paired original compound eyes in arthropods, for example, in xiphosurans.

FACTS

It is commonly believed that an arrangement in two transverse rows of eight eyes is plesiomorphic. Only two weak aspects support this view, however: (a) there is no reason at all to doubt that the presence of eight eyes forms part of the araneid ground pattern, and (b) their arrangement in two rows is widely observed both in the Mygalomorphae (for example the Actinopodidae; see Simon, 1892: 79, figs 81-83) and in the Araneomorpha (for example Araneidae, Eusparassidae, Thomisidae).

On the other hand, lateral eyes more or less distinctly grouped in triads occur in various groups of spiders. Mesothelae, Migidae and Hypochilidae have already been mentioned. Almost perfect triads occur in Pholcidae (Fig. 4f). The same is true of Amblypygi (Fig. 4b) and Uropygi, the direct outgroups to spiders!

The arrangement of the eyes in the extinct Trigonotarbida deserves special attention. According to Selden *et al.* (1991: 254), they form the sister group of all other pulmonate taxa (=

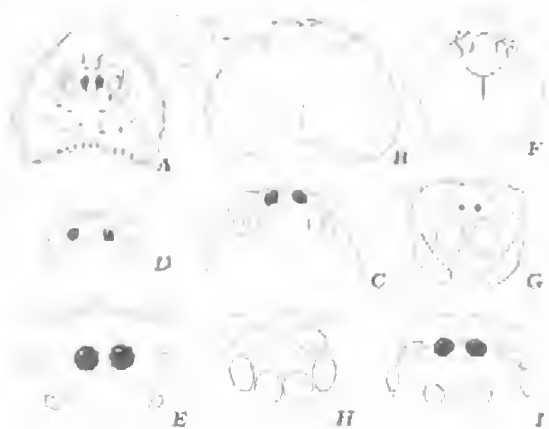


FIG. 4. Position of median (black) and lateral eyes in Trigonotarbida, Amblypygi and Araneae. A, Trigonotarbida: *Gilboarachne griersoni*, reconstruction of prosoma (from Shear *et al.*, 1987). - B, Amblypygi: *Damon* sp. C, Hypochilidae: *Hypochilus geritchi*. D, Atypidae: *Atypus affinis*. E, Migidae: *Poecilomigas* sp. F, Pholcidae: *Pholcus circularis*. G, Mesothelae: *Liphistius* sp. H, Dysderidae: *Dysdera* sp. I, Agelenidae: *Agelena* sp. (Not to scale).

Araneae + Amblypygi + Uropygi + Schizomida). Devonian trigonotarbids had the usual two median eyes, and the lateral eyes were represented by up to 9 (12 ?) lenses (Fig. 4a). Three of these were major lenses, while the others were minor lenses arranged in the interspace between the major ones (Shear *et al.*, 1987). This kind of transformation of the original compound eyes clearly indicates that a triad of major lateral eyes is a feature of the ground pattern of the pulmonates as a whole; accordingly, the loss of the minor lateral eyes could be regarded as an autapomorphy of all other pulmonates, including spiders. This secondary reduction of the minor lateral eyes may explain why most triads are not perfectly closed, not even in amblypygids (Fig. 4b).

The peculiarity 'lateral eyes in triads' is commonly used as a character in spider identification keys, but as far as we can tell, its potential bearing on phylogeny has never been discussed. Could it be that triads of lateral eyes are part of the ground pattern in the Araneae?

A survey of how the lateral eyes are positioned in representatives of higher taxa of spiders shows that almost perfectly 'closed' triads (as in pholcids) are rare. In most instances, the three lateral eyes on each side are somewhat dissociated. In addition to the Mesothelae and Migidae already mentioned, we should also like to draw attention

to the Atypidae (Fig. 4d) and to the illustrations in Raven's comprehensive study of the Mygalomorphae (1985). In many cases the posterior lateral and the posterior median eyes are closely connected, with some distance between them and the anterior laterals. *Hypochilus* shows slightly dissociated triads (Fig. 4c). The Dysderidae (Fig. 4e) and Oonopidae are six-eyed spiders, having the median eyes completely reduced. In dysderids, the lateral eyes are closely grouped together, resembling the arrangement of the laterals in the Mesothelae. In many groups within the Araneomorphae, diads are present instead of triads. They are formed by the ALE + PLE, with the PME separated. This arrangement can be found in Austrochilidae and especially in most Theridiidae and Linyphiidae, for example. Diads also occur in groups characterized by a secondary loss of the PME, such as Scytodidae.

INTERPRETATION

The assumption that eight eyes arranged in two transverse rows were already present in the ground pattern of the Araneae is not supported by any concrete fact; nor would this at all correspond with the situation in the nearest outgroups. It would mean that triads and triad-like arrangements of the lateral eyes in spiders were classifiable as parallel developments (homoplasies). This is unlikely. In accordance with the position of the eyes in the Amblypygi and Uropygi, we expect that the laterals were primarily grouped as triads (ALE + PLE + PME). This hypothesis is supported by five arguments:

a) Triads of major lateral eyes (lenses) already existed in Devonian Trigonotarbita; hence, triads apparently form part of the ground pattern of all pulmonates among arachnids.

b) The postulated configuration is in good agreement with the arrangement of the eyes in the direct outgroups.

c) Triads and semi-triads present in various groups of the Mygalomorphae and also of the Araneomorphae must no longer be explained by assumed parallel origin.

d) Various types of somewhat dissociated lateral eyes can be explained by a secondary separation of the ALE or of the PME from the others, which frequently remain in contact with each other.

e) Simon's 'oculi laterales utrinque contigui'

(e.g., 1894: 517), that is to say, the occurrence of diads can be explained as part of the original triad.

To some extent, the question remains open, as to how it is possible to distinguish between eye positions that can be regarded as more or less modified triads and other positions, with secondarily approximated ALE and PLE.

PERSPECTIVES

Apparently, plagiognathy is part of the ground pattern of the Araneae. Developments in the directions of orthognathy and labidognathy can easily be explained as divergent evolutionary changes (Fig. 3). The question therefore arises of how these might be correlated with functional aspects. As an impetus for further discussion, we propose the following working hypotheses:

a) In the Mygalomorphae, orthognathy may be correlated with the capture of prey on the ground. Under such conditions, the two parallel fangs of the chelicerae can easily penetrate the victim on a substrate like two stabs of a dagger. It seems remarkable that a semi-orthognathous position of the chelicerae has originated secondarily in the Dysderidae: they kill woodlice on the substrate.¹

b) In the Araneomorphae, the origin of labidognathy may be correlated with the evolution of capture webs (sheet, frame, orb webs etc.). These could make it more efficient to bite the prey with two opposing chelicerae or fangs, whereas plagiognathous and, even more, orthognathous chelicerae might not penetrate but rather push away the victim: there is no longer any substrate 'supporting' prey animals.

c) Plagiognathy and the maintenance of lateral triads or semi-triads of eyes apparently form part of the ground pattern of spiders; these features are confined to more 'primitive' groups. The presence and the various types of transformation of these two characters should be integrated into current concepts on the phylogeny of the Araneae (see, for example, Raven, 1985; Coddington, 1990). At present, our view of features of an araneid ground pattern and succeeding evolutionary changes seems to be somewhat at odds with various published cladograms; they hence could be partially wrong. We feel that this conflict may be due to the possibility that characters assumed to be synapomorphies in various cladograms (see,

¹ But see Kaestner (1953a: 62). He believed that the position of the chelicerae in *Dysdera* was a 'phylogenetic link' between orthognathy and labidognathy. Unfortunately, he was not aware that the first postembryonic stages were nearly labidognathous, with relatively shorter basal segments and only slightly oblique fangs (pers. observ.). In *Dysdera*, the final semi-orthognathous position was gradually acquired in later instars.

e.g., Platnick and Shadab, 1976, fig. 1; Raven, 1985, fig. 1) may well turn out to be symplesiomorphies; e.g., Raven's characters 35 (eyes spread widely across the prosoma; same as Platnick and Shadab's character 1) and 36 (male pedipalps: conductor of bulb present; see Kraus, 1978, figs 12, 14-16).

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